

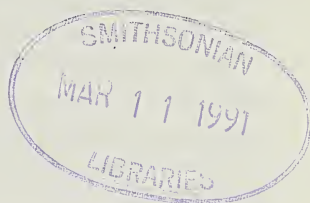
## Mating Behavior and Male Investment in *Euphydryas anicia* (Lepidoptera: Nymphalidae)

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**Abstract.** The size of male ejaculates in butterflies have often been suggested to play a key role in shaping the characteristics of butterfly mating systems. Females might choose males with larger ejaculates (greater nutrient investment), but a large ejaculate may be more costly for the male to produce. It remains unclear how various factors may interact to determine the size of male ejaculates. Rutowski (1984) called for tests over a range of species, including ones with unusually large or small nutrient investments. We studied mating behavior in *Euphydryas anicia*, which has an unusually small spermatophore (<2% of body weight), and suggest that spermatophore size relates strongly to many aspects of the mating system: male and female choosiness, female mating frequency, and the length and complexity of courtship.

### Introduction

In some butterflies males transfer sperm and nutrients through mating to females (eg. Boggs and Gilbert 1979, Engebretson and Mason 1980, Walker 1980, Boggs 1981, Boggs and Watt 1981). A range of sizes exists for male ejaculates among species (Rutowski et al. 1983), and it has been suggested by many authors (for review, see Thornhill and Alcock 1983) that the size of the male nutrient investment plays a key role in shaping the characteristics of the mating system. Females would presumably prefer males with larger nutrient investments. Rutowski (1984) cautions that "untested assumptions underlie this conclusion" and that "students of the mating behavior of butterflies and moths should pay special attention to species whose males...produce [un]usually large or small nutrient investments". One major untested assumption, for instance, is that offspring benefit from the nutrients transferred at mating. In studies on a moth (Greenfield 1982) and a butterfly (Jones et al. 1986), it was found that female fecundity was in

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fact not a function of the size of male ejaculate weight. Without a positive correlation between male ejaculate size and female fecundity, it is difficult to argue that males with larger spermatophores are more attractive to females.

Male ejaculate size may also affect the mating system through male choice. Recent evidence suggests that males incur non-trivial costs in producing ejaculates, that the number of ejaculates they can produce is limited, and therefore some discrimination should be expected with respect to their patterns of allocating ejaculates (eg. Marshall 1982, Dewsbury 1982, Svard 1985, Svard and Wilklund 1986). Rutowski (1985) studied choice in *Colias eurytheme* males which pass about 6% of their body weight (cf. Rutowski et al. 1983) to females at mating, and found that the size of females accepted by males is less variable than that of rejected females, implying choice by males. We studied the behavior of a butterfly with a very small spermatophore (<2% of male body weight), *Euphydryas anicia*. By following individual *Euphydryas anicia* in the field we were able to collect data on mate location behavior, mate discrimination, and courtship complexity and duration. Dissection of mated females gave information on spermatophore size and mating frequency. Our results support the prediction by Svard (1985) that males of monandrous species will tend to have small spermatophores, and may be compatible with those of Rutowski (1985) because of the difference in the size of the investment by the males of the two species studied. Like Rutowski's study, ours may support the notion that the size of the investment may be reflected in the degree of male choosiness. We discuss possible reasons for the small spermatophore in *E. anicia*, and discuss how a small spermatophore relates to other characteristics of the mating system.

### Materials and Methods

*Euphydryas anicia* Doubleday and Hewitson occurs in scattered populations over the western half of the United States (White 1979, Cullenward et al. 1979, Ferris and Brown 1981). Near Red Hill Pass, 11 km east of Fairplay, Park County, Colorado, a population occurs in a part of a very flat, high altitude (2,900 m) intermontane plain (Odendaal et al. 1988). This site is an approximately 700 × 1300 m area containing a relatively localized population of *E. anicia*. The flight season is very short. Several years of site observations show that after snow has melted (early to mid-May) postdiapause larvae feed on *Besseya plantaginea* and *Castilleja integra* (Scrophulariaceae), pupate, and emerge as adult butterflies in mid-June. About four to five weeks pass from first emergence to the last butterfly. For the first several days there are only males as occurs with other *Euphydryas* (Iwasa et al. 1983). Butterflies from this site contain bitter iridoid glucosides sequestered during larval consumption of the host plants (Stermitz et al. 1986, Gardner and Stermitz 1988). Host and nectar plants are distributed throughout the site, although patchily in some years. All plants on the site are low-growing and herbaceous, with consequent excellent visibility for observing and censusing larvae, pupae and adult butterflies. During the 1985 flight season we conducted a mark-release-recapture program, capturing and marking 1260



males and 671 females. The first males were observed on June 13 and the first females on June 17, with an approximate 50:50 ratio reached on June 27. Behavior was observed during the entire flight season and some additional observations were conducted during the 1986 season.

## MALE MATING BEHAVIOR

Individual field-collected males were marked and followed by two researchers, one recording behavioral events with a hand-held Radio Shack TRS 80 computer while the other marked landing spots. Males were recorded as collecting nectar, sitting, flying and chasing virgin females, previously mated (plugged) females, other males or other species.

## FEMALE MATING BEHAVIOR

Because lab-rearing or tethering virgins may alter their behavior (Odendaal, unpublished data; M. Singer, personal communication), we followed unrestrained field-hatched virgins. Thirty-one virgins were encountered flying or just emerging from pupae in the field. Some were followed immediately, others were caught and released later the same day, while still others were kept for up to two days in a cage and fed with a mixture of honey and water (see Jones et al. 1986). One or two observers followed each virgin, noting and timing each type of behavior, and marking each landing spot with a numbered flag when possible. As a measure of relative local male density at various landing spots, all males passing within 1.5 m of a sitting virgin were counted. The same procedure was repeated with twelve field-collected plugged females.

Behavioral data for females were analyzed with an ANOVA to show whether a significant amount of variance in each of the parameters (flight frequency, average flight distance, local male density, number of male chases and chase distance) could be explained by female type (previously mated or plugged females, virgins that mated as a result of a male chase, and virgins that did not mate). Fischer's Least Significant Difference Test was performed for each parameter to determine whether the means of the female types differed significantly from one another.

## SPERMATOPHORE DATA

Virgins that were mated were dissected within several hours of mating to obtain spermatophores, or were kept in a refrigerator, until dissection a few days later. Refrigeration slows down absorption of the spermatophore (C. Boggs, personal communication), and a truer assessment of the original spermatophore condition and weight is obtained. Forty-two field collected females were dissected for comparison. Spermatophores were described as full, half full and empty (when only a crust remained). Excised spermatophores and butterflies were dried at ambient lab temperature and low humidity. Our data using dry weight spermatophore to dry weight butterfly comparisons correlate extremely well with recent data for *E. editha* and *E. chalcidona* (Jones et al. 1986), where wet weight comparisons were used, presumably because both spermatophores and butterflies are approximately 75-85% water. The use of wet weights was suggested (Rutowski et al. 1983) to be of value since water has been considered a "nutrient" for female eggs (Marshall 1982b). This is not likely for *Euphydryas* species where water contributed from the spermatophore would represent an

insignificant portion of that present in the egg and where water has been shown to play no direct role in enhancing fitness in females (Murphy et al. 1983).

## SIZE AND AGE OF INDIVIDUALS

The length of the forewing was used as a size measurement. Wing wear, as an estimate of age, was determined for all females using a five point rating system (1 = extremely fresh, 2 = fresh, 3 = medium, 4 = old or worn, 5 = extremely worn; see Iwasa et al. 1983). Wing length and wear estimates were also obtained for males from field-captured mating pairs, and for 35 field-caught males.

## WEATHER DATA

The condition of the weather was recorded about every fifteen minutes, or whenever it changed, by using the simple denotations *fair* (sunny, with little or no wind), *marginal* (largely cloudy with little sun or windy) and *bad* (heavy clouds or very windy). At least some butterflies were active during all three weather classes. When the weather became very bad, such as when wind was extremely strong or it was raining, no butterflies were active, and few were ever active if the sun was obscured for any length of time.

## Results

### MALE BEHAVIOR (Table 1)

Males tend to chase all flying objects vaguely the size of a *Euphydryas* butterfly, including other insects such as grasshoppers (for male behavior see also Odendaal et al. 1988, 1989). Males often chase other males, engaging in frantic erratic flights during which the original object of the chase is often replaced by another. Some of these flights included mating attempts. One extreme male-male chase lasted 22 minutes and involved numerous mating attempts, during which the pursuing role often switched and brief copulations were achieved three times.

From a total of 119 male chases recorded (Table 1), virgins were found to be chased longer than plugged females ( $p < .005$ , Mann-Whitney U-test), and plugged females were chased longer than males ( $t = -2.4488$ ,  $p < 0.02$ , Mann-Whitney U-test for large sample sizes see Siegel 1956); males were not chased significantly longer than other species ( $t = 1.5088$ ,  $0.1 < p < 0.2$ , Mann-Whitney U-test). The extreme 22 minute male-male chase was not included in these data as males often switched pursuing roles, which made it difficult to time individual chases.

Males responded readily only to flying objects. They often flew within centimeters of sitting virgins or plugged females or even walked around on the same inflorescence with such females without reacting to them. Only when the female took flight would the male chase her.

### FEMALE BEHAVIOR (Table 2)

*Virgins that mated*—Twelve of the 31 virgins mated in an average of 31 minutes after release. Of these, nine mated after an aerial pursuit by a male. In a typical case of these nine, a virgin sat for a while on a plant



Table 1. Summary of the duration of different types of male chases: males chasing non-specifics, males chasing males, males chasing females, and males chasing virgins.

Object of male chase:	heterospecific	male	mated female	virgin female
n	60	51	25	2
ave(sec)	2.86	3.72	11.96	98
S.D.	2.41	3.63	12.18	26.87

Table 2. Behavior data for females and ANOVA showing whether a significant amount of the variance in each of the parameters can be explained by female type. Asterisked entries have means that do not differ significantly (at.05 level) according to the Fisher's Least Significant Difference Test. Male density = Number of males passing within 1.5 m of a female per minute.

Behavior Parameters	FEMALES TYPE			F	df	P
	Plugged Females (n = 12)	Virgins that Mated (n = 12)	Virgins not Mated (n = 19)			
Flights per hour	15.50* ± 9.99	14.17* ± 16.42	2.79 ± 3.31	4.02	2,35	ns
Flight Distance(m)	20.91* ± 16.20	14.91* ± 9.64	12.00* ± 13.59	4.83	2,25	ns
Male density	1.12 ± 1.98	9.52* ± 9.86	10.23* ± 7.73	7.15	2,35	p<.01
Male chases/min	0.83* ± 1.03	0.83* ± 0.58		0.00	1,22	ns
Chase Distance(m)	5.30* ± 8.87	20.20* ± 21.01		4.27	1,18	ns

or on the ground and then made a short flight. Almost immediately a male gave chase. They landed, he crawled behind her, bent his abdomen, and they mated, achieving the straight back-to-back position within one minute of landing. Of the remaining three virgins, one was crawling on the ground, a second was collecting nectar and the third was hardening her wings after eclosion when mated. In these cases males landed virtually on top of the females, seemingly by accident. All virgins were mated by the first male that attempted mating and only one seemed to resist briefly by walking away a few centimeters prior to being mated.

During the 1986 season, two additional females were observed from eclosion to mating. Both had wings that had not hardened yet and were

sitting a few centimeters above empty pupal cases when encountered in the field. One mated 98 minutes and the other 101 minutes after observation began. In the first case, 68 males passed within 1.5 m and several less than ten cm from the virgin without reacting to her. Finally one male landed virtually on top of the female and they mated immediately. In the second case, 105s male passed within 1.5 m. Four short flights of less than 20 cm each were taken when no males were present, followed by a 10 m flight, during which one male and then a second chased her. She alighted and both males attempted to mate her, with one succeeding after about one minute.

As an additional measure of female choice we recorded wing size and condition of males. These factors did not differ significantly between 12 males that mated and 210 males collected during the same period (size:  $t = 1.9178$ ,  $p < 0.05$ ; condition:  $t = 0.6723$ ,  $p < 0.05$ ).

*Virgins that did not mate*—Nineteen out of 31 virgins did not mate during the time of observation (approximate one hour cut-off, usually due to unfavorable weather). Sixteen of these were never chased by males. Those that flew did so significantly less often and for shorter distances than virgins that mated (Table 2). Seven did not fly at all as opposed to only one of those that mated. Three virgins were lost from observation while being chased by males. One was pursued simultaneously by four males who also scrambled trying to mate with one another during the chase. The number of males that passed within 1.5 m of the virgins (relative male density) did not differ significantly between virgins that mated and those that did not (Table 2). In the cases of five non-mated virgins, males literally crawled over them or were side-by-side while obtaining nectar.

*Previously mated (plugged) females*—Plugged females flew greater distances and more frequently than virgins, but this was significant only in comparison with virgins that did not mate (Table 2). When pursued by males in flight, plugged females continue flying, trying to evade the males. If unsuccessful, they land and energetically flutter their wings during mating attempts. Six of the 12 plugged females were chased by males, two of them twice and one three times. None mated. (This nonreceptivity was observed many additional times during the 1986 season when we followed thirty-one plugged females in a detailed study of their behaviour and movement; see Odendaal et al., 1989. Plugged females fly differently from virgins. Once they have begun laying eggs, their abdomens become noticeably slimmer and their flight is smoother and stronger. Male density around plugged females was significantly less than around virgins ( $p < .01$ ), but males chased both groups equally readily.

*Spermatophore weights and condition* (Table 3)—All twelve freshly mated females were dissected and classified as having full spermatophores. Dissection of 42 plugged females of various ages collected in the field over the season yielded only three that had mated twice, each



having two spermatophores. Of the 39 females that mated once, five had very old, shriveled spermatophores and near-empty bursas, whereas the remaining 34 had full or half full spermatophores. Of the three twice-mated females, two had one old and one fresher spermatophore and the third had two freshly deposited spermatophores. The ages of the three twice-mated females ( $x = 2.33$ ) did not differ significantly from that of the 39 females ( $x = 2.76$ ) that mated only once ( $t = 0.5617, p < 0.5$ , Mann-Whitney U-test for large sample sizes; see Siegel 1956).

Virgins had a condition of 1 which differed significantly from the average condition of 2.69 of field caught females ( $t = 6.1984, p < 0.001$ ). Female body weight also differed significantly between the two groups ( $t = 4.0572, p < 0.001$ ), and body weight regressed significantly on condition (age),  $F = 49.8804, p < 0.001$ . Spermatophore weight or % dry weight did not differ between the groups, and neither variable regressed significantly on condition (age).

A group of 43 field collected males were dried and weighed, with average weight being  $27.7 \pm 5.1$  mg. The range was 16.2 to 38.0 mg. The average spermatophore weight (Table 3) thus represents about 2% of the male body weight.

*Effect of weather*—The weather had a profound effect on behavior. When it was raining, or cold and cloudy, no butterflies were active. Butterflies were clinging to plants when it was too cold or windy to fly and could easily be picked up by observers. A few butterflies still showed sporadic activity when we classified weather as bad, and more when we considered the weather as marginal. We estimated about 56 percent of all potentially available time (daylight hours) to be good, about 29 percent to be marginal, about 3 percent to be bad, and about 12 percent of the time as too bad for any activity at all. To illustrate the effect of

Table 3. Summary of spermatophore data that were obtained from dissections of field-caught plugged females and lab-mated virgins.

		Age (days)	Body Weight (mg)	Spermatophore Weight (mg)	% Dry Weight
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Field-caught females (n=42)	x	2.69	36.3	0.48	1.3
	S.D.	0.84	9.5	0.28	0.83
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Lab-mated virgins (n=12)	x	1	48.8	0.64	1.3
	S.D.	0	9.2	0.37	0.66
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t-value			-4.0572	-1.6501	0.010795
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Significance level			1.6700 <sup>-1</sup>	0.01049 ns	0.9144 ns
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slight weather changes on male butterfly activity, we plotted the number of male butterflies chasing females, other males or non-specifics/ unit time for good and marginal weather (Figure 1).

Discussion

There remains a “specific lack of field data to understand the selective advantages behind the evolution and maintenance of large nutritive spermatophores” (Wickler 1986). This study shows that spermatophores in Colorado *Euphydryas anicia* are very small compared to those species investigated by Rutowski et al. (1983). What are the possible reasons for the small spermatophore size in this species?

Svard (1985) showed that male *Pararge aegeria* invested only about 1.4% of their weight under laboratory conditions, and explained this in terms of *P. aegeria* being a monandrous species with the male supplying only enough sperm to fertilize all the eggs of the female. The problem with this hypothesis is that the males in that study still produced 74% of material other than sperm. However, our data on female mating frequency do support the Svard explanation in that females in our field

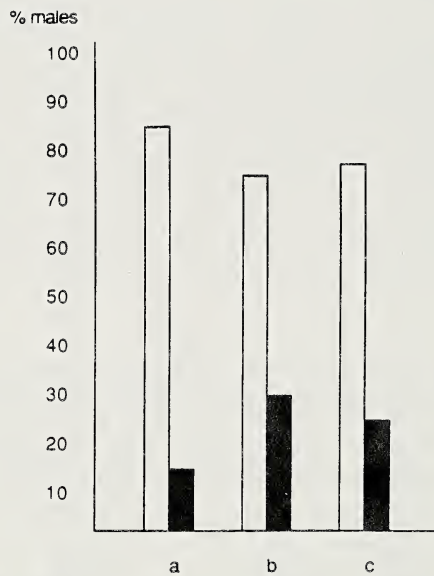


Fig. 1 Comparison of male behavior in good and marginal weather.

Thirty-three *Euphydryas* males were followed in good weather for a total of 527 minutes and fifteen males in marginal weather for a total of 520 minutes. It was recorded whether they chased or ignored other males, females, and non-specifics that flew within a radius of 1.5 m past them. Clear bars indicate percentage of (a) other males, (b) females, and (c) non-specifics that were chased in good weather and solid bars percentage of passerby butterflies chased in marginal weather.



study showed a very low degree of polyandry (cf. Ehrlich and Ehrlich 1978).

The length of the breeding season may be one link between the environment and mating system characteristics (Odendaal et al. 1985a). In species with very short breeding seasons, females may be limited by the availability of time for repeated matings, host plant search and oviposition and should produce eggs mainly from resources acquired during the larval stage. The general picture in *Euphydryas*, which has a short breeding season (Iwasa et al. 1983), appears to support this. Singer and Ehrlich (1979) showed that only the offspring of the first egg batches have time to reach diapause in California *E. editha* before host plants senesce, and Murphy et al. (1983) showed that nutrient substances ingested by adults only slightly benefit later egg batches. Furthermore, Jones et al. (1986) showed that the size of the male investment does not affect female reproductive output in *E. editha*. In contrast, female *Colias* butterflies did show reduced reproductive output with reduced male investment (Rutowski et al. 1987). On a high altitude plain in Colorado, time for locating and choosing host plants may be even more limited for *E. anicia* than for California *Euphydryas* because of lower temperatures and the frequently unfavorable mountain weather. Monandry may be advantageous. Male mating success is largely determined by access to fertilizable females (cf. Iwasa et al. 1983, Odendaal et al. 1985a) and if females tend to be monandrous, rapid mate acquisition may be crucially important to males. Viewed in this background, several points emerged from this study that may be related to a small male ejaculate:

(1) *Low level of mate discrimination for males and females*—Very limited time for locating and choosing host plants may have led to monandry in *Euphydryas* females. Females on this site use considerable time locating hostplants, then sometimes as much as an hour inspecting various plants and up to another hour laying eggs. This process is often interrupted by unfavorable weather. Monandry and a low level of female discrimination will place a high premium on rapid mate acquisition by males which may lead to a low level of male discrimination. Male *E. anicia* pursue any flying object that might possibly be a conspecific female. Males also chase and try mating with one another. That these are true mating attempts is corroborated by the observation of brief amplexes between males. Males generally do not approach sitting males, females or even virgin butterflies but chase almost any insect that flies, presumably to maximize their chances of encountering fertilizable females. The data indicate that males follow virgins more persistently than plugged females, which in turn are followed more persistently than males. Odendaal et al. (1985b) suggested that there may be a close contact pheromone for identification of sexual partners, but since males also try to mate with males and plugged females it is

highly unlikely that males would discriminate among individual virgins in the field.

Similarly, females of *E. anicia* can hardly be regarded as discriminatory. All twelve virgins in 1985 and the two observed in 1986 accepted the first male almost immediately. These males were not larger than average. Rutowski (1984) builds a strong case for mate choice in the lepidoptera on the basis of nutrients passed from males to females in many species (eg., Boggs 1981; Rutowski 1982; Marshall 1982b). Females should select among males on the basis of traits (such as size) which indicate that they can provide a large nutrient investment (Thornhill 1976). This apparently is not true of *E. anicia*, presumably because of the small spermatophore produced by males, or because females acquired sufficient nutrients for egg production while in the larval stage (cf. Murphy et al. 1983). Jones et al. 1986 showed no relation between spermatophore size and reproductive output in *Euphydryas editha* and *E. chalcidona*.

(2) *Males exhibit scramble competition*—Time-constrained males of explosive breeders evaluate the quality of mates quickly if at all, and sometimes males seem unable to discriminate visually between males and females (Odendaal et al. 1985a). In four of the twelve virgins we observed mating, more than one male followed the virgin, and in three cases males scrambled intensely for her. One of the virgins we lost escaped when four males who followed her scrambled and tried to mate with one another. In 1986 we observed eight or nine males scrambling for a single virgin. Similar frenzied mating attempts were also observed with caged males (Odendaal and Ehrlich, unpublished data).

(3) *Spermatophore size and female mating frequency*—As predicted by Svard (1985) for monandrous species, *E. anicia* spermatophores are very small relative to their body size. They are smaller than any recorded in the available literature (Rutowski et al., 1983). Females of the study population also remated very infrequently, with only three (7%) of field-caught females having more than one spermatophore. Furthermore, one of these females contained two fresh spermatophores and this could have been the result of scramble competition rather than a female tendency to remate. In a laboratory experiment Odendaal (unpublished data) once observed a virgin copulating with two males. Males often try to displace a mating male, and this may result in two spermatophores as the plug of the first one may not have hardened yet (Labine 1964). Percentage of the body weight made up by spermatophores did not differ between randomly collected mated females and freshly mated females, suggesting that females did not gradually use substantial amounts of the spermatophore for nutrition.

(4) *Length and complexity of courtship*—Rutowski (1984) states that nutrient investment made by male butterflies appears to have given rise to selection pressures that have shaped courtship behavior of males and perhaps females. Supportive data comes primarily from pierids (see



Rutowski 1984). Because of the small male investment in *E. anicia*, it may not be surprising that courtship is essentially non-existent in this population. All copulations were closely observed, sometimes from less than a meter away, and a successful mating merely involved the curling of the male's abdomen, sometimes a second or two searching for the female genital aperture with his genitalia, and copulation, which we regarded as complete when the couple achieved the straight back-to-back position. A further twenty copulations of caged butterflies obtained from this site and filmed on video tape yielded essentially the same results (Odendaal and Ehrlich, unpublished data).

Our work deviates somewhat from data on the *Euphydryas* species. The female remating frequency at Red Hill was considerably less than that for *E. editha* in California (Labine 1964) and there was a striking difference between relative spermatophore weights in the present work (<2%) as compared to that reported (10.8%) for three *E. chalcedona* individuals in Arizona (Rutowski et al., 1983). A detailed comparison of mating behavior of species within the genus *Euphydryas* would provide an interesting test of predictions on how spermatophore size may affect mating systems.

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